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PATTERNS IN THE SPATIAL AND TEMPORAL USE OF TEXAS MILKWEEDS (ASCLEPIADACEAE) BY THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L.) DURING FALL, 1996

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ABSTRACT. In an attempt to better understand the fall migration of the monarch butterfly (*Danaus plexippus* L.) through Texas, the spatial and temporal distribution of milkweeds and immature monarchs were monitored along an 800 km transect. Important monarch host plants were found to be distributed unequally along the transect. Breeding monarchs were present at least one month before the main body of migrants appeared. The distribution of eggs and larvae did not spatially follow the distribution of milkweeds. Some milkweed species and locations were used more than others. Possible explanations for the distribution patterns observed include the circumscribed nature of the fall migratory pathway and the foraging efficiency of the polygyne version of the imported fire ant.

Additional key words: natural regions, oviposition, fire ant, *Solenopsis invicta*, *Asclepias*, migration.

Although the monarch butterfly (*Danaus plexippus* L.) is the best known of North America's migratory insects, much remains to be learned about the spatial and temporal patterns of how it populates and then vacates northern North America each spring and fall (Brower 1995). Our basic understanding of this process is as follows: During summer, the eastern group of monarchs spends two or more generations breeding in North America above latitude 35° (Malcolm et al. 1993). In late summer and early fall, the progeny of summer breeders migrate to central Mexico, crossing much of the North American continent (Urquhart 1987). They spend five months at the Mexican overwintering sites, most of the time in a state of reproductive dormancy. After mating in late winter and early spring, they fly northward to once again exploit the milkweed flora (Cockrell et al. 1993) widely distributed throughout North America (Woodson 1954). During spring and summer in their northern breeding grounds, they greatly increase their numbers, reversing the population decline that occurs during fall and winter.

To understand more about monarch population dynamics in Texas and the implications for the monarch population of North America, this study investigated the presence and abundance of monarch immatures on milkweed flora (Asclepiadaceae) in Texas during the fall of 1996.

MATERIALS AND METHODS

Milkweeds were examined along two routes between 30°N and 32°N latitude. One route extended east from Austin to Pineland in Sabine County in extreme eastern Texas near the Louisiana border and the other extended west from Austin to Ozona in Crockett County in West-central Texas (Fig. 1). A loop was made at the eastern end to insure that areas where single-queen (monogyne) fire ant colonies had been reported were well covered (Anonymous 1998; E. Vargo, pers. comm.). The two segments combined, referred to below as the cross-Texas transect, stretched about 60% of the way across Texas from 31.25°N, 93.985°W at Pineland to 30.00°N, 101.201°W at Ozona, a distance of 801.66 km (ca. 900 road kilometers; see Marvin 1939, Table 92). The transect was traversed three times during the fall migratory season. The east and west segments of the first transect were conducted on 20–23 September and on 27–29 September respectively. The second transect was conducted on 6–7 and 11–13 October and the third on 12–13 and 12–13 November. On the first transect to West Texas (27–29 September), the return route was slightly different from the two subsequent transects. Instead of proceeding directly to Austin along Highway 290, a parallel route 30 km to the south of the regular route was taken. This route followed Interstate 10 to Comfort and then proceeded eastward along Highways 473, 281 and 165, rejoining Highway 290 at Henly. The last transect to East Texas (12–13 November) ended at Madisonville. The transect was truncated here because no activity had been observed on the previous transect (6–7 October), and none had been observed prior to Madisonville.

The scheduling of the transects was based on Texas Monarch Watch reports of the presence of monarchs in the state. Transect dates were chosen to cover periods before the main body of migrants arrived, during the peak of the migration and after most monarchs had cleared the state. (The Texas Monarch Watch is an educational outreach service that solicits reports from volunteers concerning the presence and abundance of monarchs in the state (Calvert 1993–1997, Calvert & Wagner in press).)

The relative abundance of milkweeds was assessed along the cross-Texas transect by counting stems whenever milkweeds were sighted. During September and October, many milkweeds were in flower and their presence was very conspicuous. Sampling stops were

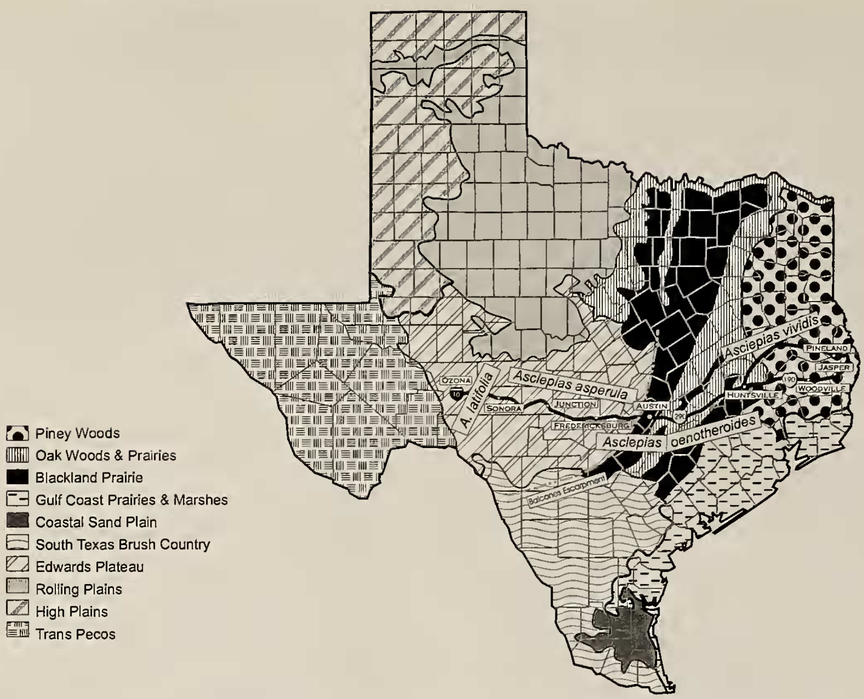

FIG. 1. The cross-Texas transect route showing the location of milkweeds important to monarch butterflies along the 800 km transect from Pineland to Ozona.

made when milkweeds were spotted in adjacent fields or roadside right-of-ways. Areas that appeared to be prime milkweed habitat such as short grass prairies and areas with poor soils were also searched. During November, when many fewer milkweeds were in flower, plants were located by revisiting areas where they were found abundant on previous transects.

This study focused on the four abundant *Asclepias* species found in central Texas: *Asclepias viridis* Walt., *A. oenotheroides* Cham. & Schlecht, *A. asperula* Wood, and *A. latifolia* Raf. Other rarer species were examined as encountered, e.g., *A. texana* Heller and *A. curassavica* L. Milkweed vines in the genera *Matelea, Sarcostemma* and *Cynanchum* were also sampled, but only sporadically. Due to the very different growth form of these species and the difficulty of following a stem through the tangle of vines, the effort of examination cannot be considered the same as for the other species.

Although every effort was made to keep the search method constant, initial search times were longer than later ones. It took less time to relocate milkweed patches after their initial discovery. Nonetheless, since the search method was always the same, the number of milkweeds counted should serve as a rough index of relative abundance of each host species in the genus *Asclepias* through space and time.

During a sampling stop, the identity of the milkweed species was verified, the stem lengths were measured, and the number of eggs and monarch larvae on the stems were counted. When available, 20 or more stems were examined. If fewer than 20 stems were present, all available stems were measured and examined. Time of day, location, and the presence of adult monarchs were also noted. Geographical locations of sampling sites were determined from a U.S. Geological Survey Map of Texas (Anonymous 1985).

A problem arose concerning the identification of eggs. At some locations in West Texas, both queen (*Danaus gilippus* L.) and monarch larvae were present at the same time during the fall. Since monarch eggs cannot be distinguished from queen eggs, eggs from both species were counted and are included the totals. Excluding the larvae present on *M. reticulata,* the host species that was used only by queens, 36% of the larvae encountered in West Texas were queens. No queen adult or larvae were encountered along the eastern segment of the transect. All eggs here were considered to be monarch.

RESULTS

Relative abundance and distribution of milkweed species used by monarchs. Approximately

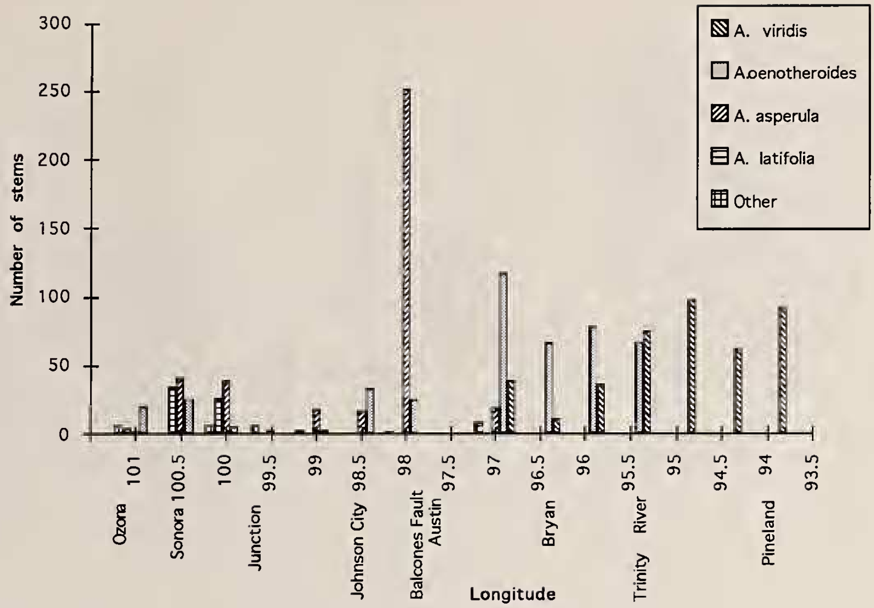

FIG. 2. The relationship between longitude and the occurrence and relative abundance of the principal monarch host plants.

midway between Ozona to Pineland, the 800 mile transect crossed a major biogeographical barrier—the Balcones Fault (Fig. 1). At the latitude of the transect, the Balcones Fault is located at Austin (97.67°W). The transect west of the Balcones Fault lies entirely within the Edwards Plateau. Elevations here are 250–300 meters higher than the transect area to the east of the fault. East of this line rainfall is ample, >32 inches per year; west of it rainfall diminishes to ca. 16 inches per year at Ozona (101.2°W longitude; Arbingast, et al., 1973). Proceeding from east to west, the transect crossed four natural regions: Piney Woods, Oak Woods and Prairies, Blackland Prairie and Edwards Plateau (Anonymous 1978). The diminishing rainfall as one proceeds westward is conspicuous in the change in natural regions, the reduced density and stature of the trees, and the change in distribution of milkweeds.

Above average rainfall during the fall of 1996 (Anonymous 1997) produced luxuriant crops of milkweed giving ample opportunity to observe their distribution and relative abundance (Figs. 1, 2). In October, when the four major hosts (*A. viridis, A. oenotheroides, A. asperula* and *A. latifolia*) were at their peak of flowering, *A. viridis* accounted for 41% of the milkweeds along the transect followed by *A. asperula* (33%), *A. oenotheroides* (17%) and *A. latifolia* (4%).

The distribution of these species along the transect varied with longitude. *Asclepias oenotheroides* had the widest longitudinal range (Figs. 1, 2). It was distributed in patches throughout most of the transect, but was not found east of the Trinity River. It appears to be mainly a prairie species, reaching its highest density in the regions between Austin (97.67°W) and Midway (95.75°W). However, it was also consistently, but rarely, encountered in the Edwards Plateau to the west end of the transect at Ozona.

Asclepias asperula was the dominant milkweed in the genus *Asclepias* on the Edwards Plateau (Figs. 1, 2). It was mainly present in patches of multiple-stemmed rosettes along roadsides and in pastures. It was found as far east as longitude 97.45°W in the Oak Woods and Prairies region between Bastrop and Austin, but east of Austin, it was rare. The highest densities were found between Austin and Johnson City. *A. latifolia* was encountered only in rare patches on the Edwards Plateau west of 100°W longitude.

The Balcones Fault at Austin divides the ranges of *A. viridis* and *A. asperula* fairly well (Figs. 1, 2). Proceeding eastward from Austin, *A. viridis* began a more or less continuous distribution around 97°W and, with two gaps, continued into the East Texas Piney Woods to the end of the transect at Pineland (93.99°W; Fig. 2). East of Austin, *A. viridis* reaches its greatest abundance in a zone extending along Highway 21 approximately 65 km on either side of the Trinity River (95.70°W longitude). This area corresponds to an area of warmer than expected temperature that extends northward along the Trinity River (Fig. 1; Arbingast, et

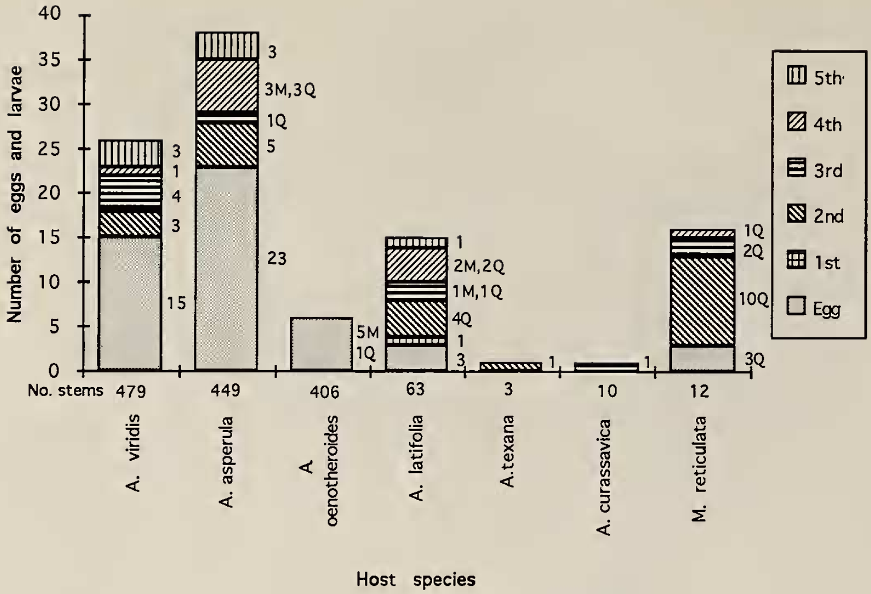

FIG. 3. Numbers of eggs and larval instars found on various milkweed hosts along the cross-Texas transect during the fall of 1996. M = monarchs (*Danaus plexippus*); Q = queen (*Dannaus gilippus*). Numbers not followed by a letter are monarchs.

al. 1973). Within this area the number of days of frost free weather are ca. 35% greater than regions above the Balcones Fault on the Edwards Plateau. The presence of dense stands of *A. viridis* corresponded well with the occurrence of Blackland Prairie and with pockets of prairies within the Oak Woods and Prairies Natural Region. Although dense stands occurred in some places within the Piney Woods, *A. viridis* in this area was confined to roadsides. Because of this restriction, its overall abundance here must be considerably less than in the prairies.

Two other milkweeds in the genus *Asclepias* were encountered along the transects. One stem of the nonnative *A. curassavica* was found in a garden in Johnson City, and three stems of *A. texana* were found along Highway I 10 at ca. 99.0°W.

Several milkweed vines were encountered in the western portion of the transects. These included *Cynanchum barbigerum* Shinners, *Sarcostemma crispum* Benth., *S. cynanchoides* Dcne., and *Matelea reticulata* Woods. Both *M. reticulata* and *S. cynanchoides* achieve high biomass in the western portions of the transect.

Stem counts of the four major milkweed species during the three months indicated that all species of milkweeds except *A. oenotheroides* declined in abundance from October to November. Only *A. oenotheroides* became more abundant at the end of the three month period. The continued growth of *A. oenotheroides* may be explained by the apparently positive response of this species to the mowing of highway right-of-ways by the Texas Department of Transportation (Calvert, unpubl. obs.).

Distribution of monarch eggs and larvae with respect to host species, location and time in the season. Prior reports to the Texas Monarch Watch indicated that in previous years, breeding monarchs had been present in low densities in Central Texas during September, and that the main mass of migrants did not arrive until the end of September. Migrants had mostly cleared the north and central parts of the state by the end of October (Calvert 1993–1997, Calvert & Wagner in press). Cross-Texas transects commenced on 21 September and continued until 18 November.

A total of 1422 milkweed stems were measured and examined for the presence of monarch and queen eggs and monarch larvae. Eggs and larvae per meter of stem were not equally distributed among milkweed species (Fig. 3). *A. texana, A. curassavica* and *M. reticulata* were infrequently encountered on the transects, but each of these species had eggs or larvae. Of the four major milkweed species encountered, leaves of *Asclepias latifolia* had the most eggs and monarch and queen larvae per meter of stem (0.73 eggs and larvae/m) and *A. oenotheroides* had the least (0.09 eggs and larvae/m). *Asclepias asperula* and *A. viridis* had 0.27 and 0.39 eggs and larvae/m respectively. Monarchs and queens used *A. latifolia* much more than any other milkweed species—almost three times more than *A. viridis* and ca. two times more than *A. asperula*.

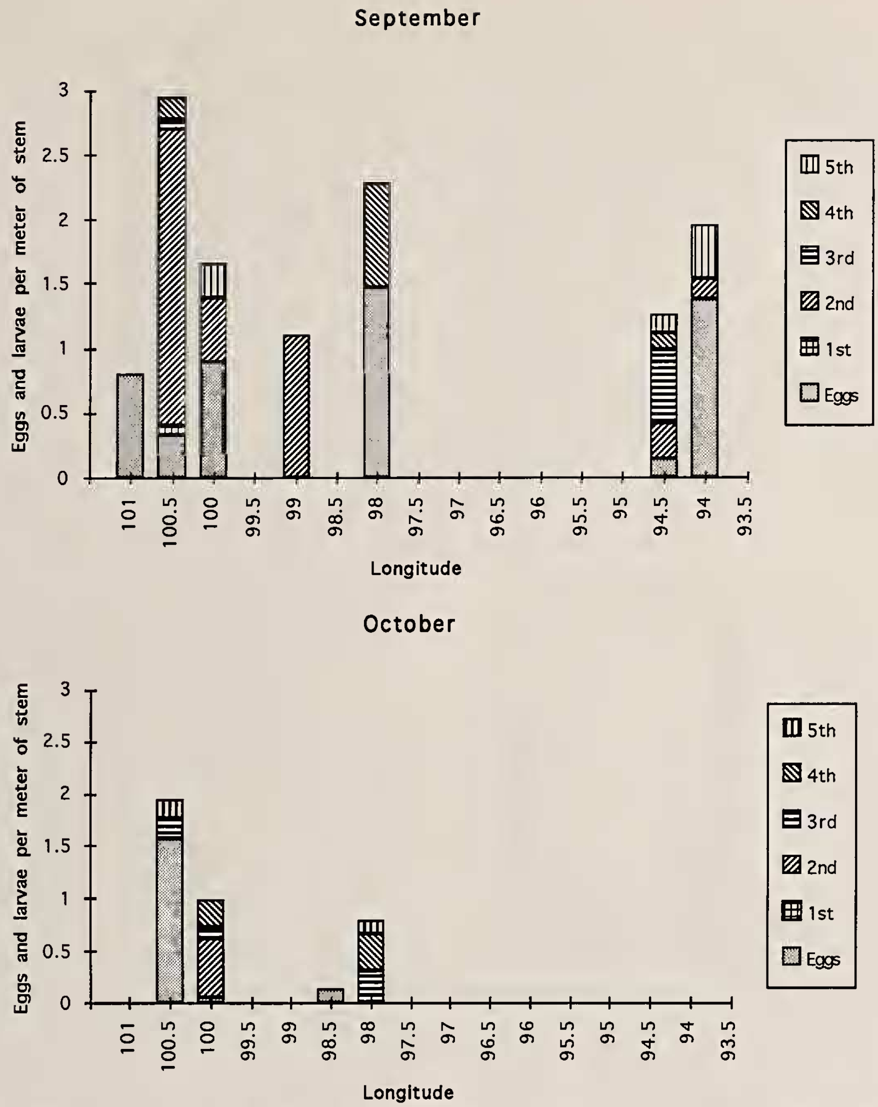

FIG. 4. The relationship between numbers of eggs and larvae per meter of stem and the time of the transect. Breeding activity declined from a high in September to near zero in November. **a,** September; **b,** October;

Most of the milkweed patches encountered were comprised of one plant species. Only rarely were two species found in the same area, e.g., *A. oenotheroides* and *A. viridis* in East-central Texas and *A. latifolia* and *A. asperula* in West Texas. Because of the spatial separation of host species, these data do not show oviposition preferences among the hosts, but rather, they show a presence in a specific geographic area.

Cursory searches of vines in the genera *Cynanchum* and *Sarcostemma* revealed no eggs or larvae. Although it has been reported that *Matelea* is not used by monarchs (P. Davis, pers. comm.), the importance of these other potential milkweed vine hosts needs to be investigated.

During the fall of 1996, the presence of eggs and larvae at both ends of the transect declined as the season advanced. Eggs and larvae were encountered on milkweeds east of Austin (97.67°W) during the initial transect of 20–23 September, but not on the two subsequent transects of 6–7 October and 12–13 November (Fig. 4a–c). In contrast, monarch and queen eggs or larvae were observed west of Austin during each of the three transects run from 27 September to 17 November (Fig. 4a–c); however, the last transect of 17–18 November yielded no eggs and only one larva. The total number of eggs and larvae for the complete transect declined from a September high of 69, to 26 in October, to 1 in November. Breeding in East Texas

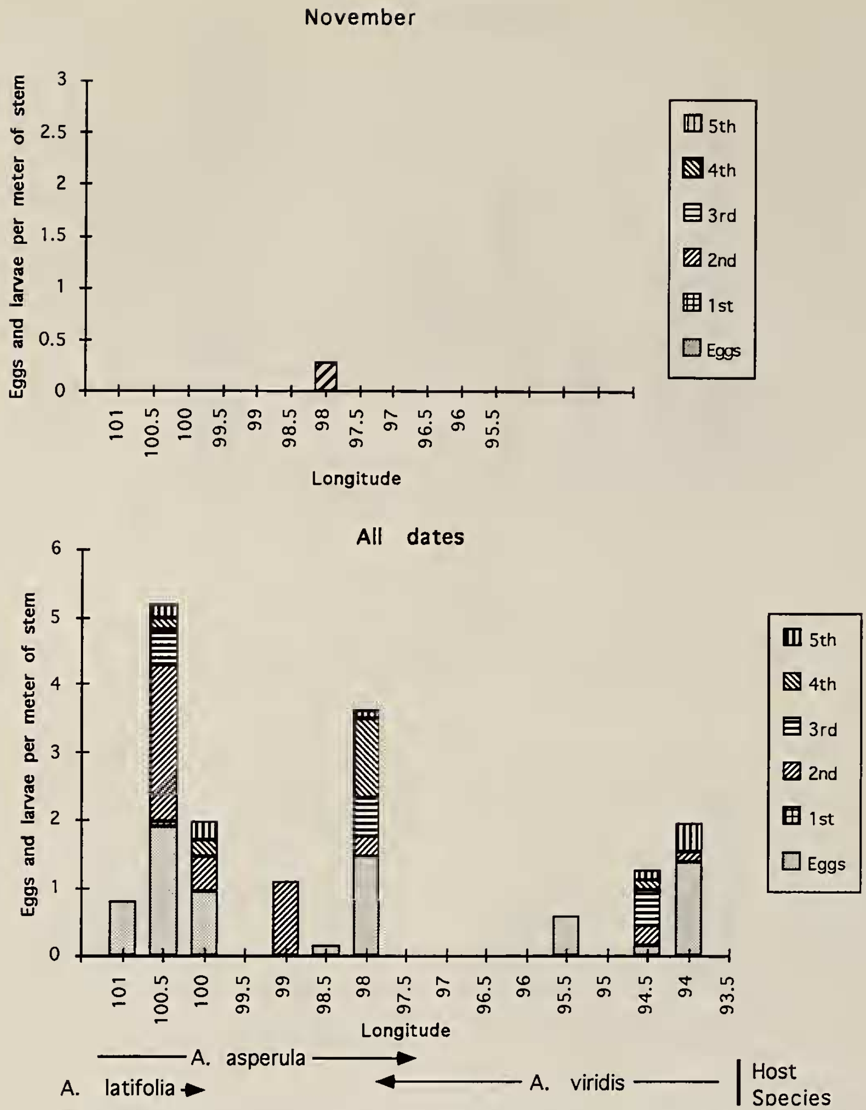

FIG. 4. **c**, November; **d**, all dates combined. A conspicuous gap in breeding activity occurs in the central prairie area between and including 96°W and 97.5°W in spite of the presence of milkweed there.

was likely over by the time the main mass of migrants arrived, but continued into November in West Texas (see discussion below).

Monarch (and queen) eggs and larvae showed a bimodal distribution along the 800 km transect (Fig 4d). The most eggs and larvae per meter of stem were found west of Austin between longitudes 98° and 101°W. The main concentration on the western end began about 15 miles east of Sonora (100.78°W) and continued to Ozona (100.96°W). Another area of concentration was south of Johnson City (98.37°W). Conspicuously and curiously absent were monarch eggs and larvae located in the center of the transect, from Austin (97.87°W) to Huntsville (95.55°W), the main prairie region of these latitudes in Texas. Traveling eastward, the number of eggs and larvae increased east of Livingston (94.63°W) and were especially concentrated in patches in the Piney Woods between Broaddus and Pineland (94.14°W). Averages for the fall of 1996 were 0.16 eggs and larvae/meter of plant stem east of Austin (n = 820 stems) and 0.47/meter of plant stem (n = 602) stems west of Austin. Most of the fall breeding activity occurred west of Austin, and most of it occurred on *A. latifolia*.

DISCUSSION

The distribution of milkweeds and monarch eggs and larvae with respect to the distribution of

milkweeds. With the exception of one major gap between Broaddus and Crockett and several minor gaps elsewhere (Fig. 2), milkweed species were continuously distributed throughout the transect. Monarch and queen eggs and larvae were not. The concentration of eggs and larvae in the eastern and western end of the transect and their absence in the middle prairies, in spite of the presence of milkweeds, requires explanation. Two possibilities are: 1) Monarchs migrating south during the fall largely avoid the east-central prairies, and therefore little oviposition occurs there. 2) The predacious activity of the imported fire ant, *Solenopsis invicta* Buren primarily determines the distribution of eggs and larvae. The first hypothesis corresponds well with data compiled from the Texas Monarch Watch. The fall migratory flyway is mainly located to the west of Austin and corresponds to the western end of the transect (Calvert & Wagner 1999). However, the migration did not reach Texas until after breeding had ceased in East Texas. Moreover, monarch eggs and larvae had already appeared in West Texas before the beginning of the migration.

The second hypothesis best explains the bimodal distribution of monarch eggs and immatures during the fall of 1996. The absence or low densities of fire ants in West Texas may explain the relative abundance of eggs and larvae in that region, while the preponderance of the far less dense single-queened colonies in East Texas (Porter et al. 1991) may allow a relatively higher number of eggs and larvae to survive there.

Other studies support the contention that fire ants are important in the decline of many species of Lepidoptera in Texas. Long term records of the presence and abundance of Lepidoptera show that the abundance of lepidopterans in the vicinity of Austin has fallen to 50% of pre-fire ant levels. Especially hard hit were grass-feeding members of the Satyridae (C. Durden, pers. comm.). During the spring of 1995, a field in South central Texas near Luling containing an estimated 1250 monarch eggs failed to yield a single late instar monarch larva (Calvert 1996). This same field contained an estimated 1001 fire ant mounds. The high mound density and renowned foraging efficiency of the imported fire ant (Porter et al. 1991) suggested that this predator was the principal culprit in decimating the monarch population. Finally, preliminary results from a study comparing larval growth inside exclusion zones, where fire ants densities were kept relatively low, to areas outside the exclusion zones, showed the production of fifth instars inside the exclusion zones to be 13 times higher than outside. (Calvert, unpubl. data).

The distribution of prairies in the mid-west and the pattern of the spring migration northward through Texas suggests that the monarchs that breed on Central Texas prairies and plains are the progenitors of monarchs that will breed on the prairies of mid-western states further north (Malcolm et al. 1993). The pattern of ample oviposition, combined with the failure of larvae to develop into later instars, found during the spring of 1995 near Luling (Calvert 1996), suggests that monarchs breeding within the fire ant zones of Texas make only a small contribution to the North American monarch population. No evidence yet exists for similar effects in areas farther east where fire ants are also abundant, but eastern fire ants colonies are mostly monogyne and are not as dense as the multiply-queened (polygyne) variety on Texas prairies (Porter et al. 1991). The reproductive success of monarch migrants passing through in the fall may be diminished for the same reasons.

Fall breeding in Texas. It has long been held that monarchs greatly increase their population size during summer months by breeding in the northern portion of their North American domain, especially in the latitudes of the Great Lakes and Northeastern States (Urquhart 1987; Malcolm et al. 1987). This is the area where the greatest biomass of one of their important milkweed hosts (*A. syriaca* L.) is found. At the peak of breeding (June and July), all females contain ovaries with numerous eggs in the oviducts and there is no communal roosting. During this period there are virtually no monarchs in Texas (Calvert 1993–1997). As the season advances into September, more and more females possess inactive ovaries and communal roosting increases. At the beginning of their southward migration, most individuals show inactive ovaries and testes, but occasionally males and females with active reproductive organs are encountered (Brower 1985). It was recognized that some breeding did occur on the way south in states such as Texas, but the extent and importance of this was not known (Urquhart 1987).

These data show that most fall breeding occurred early in the cycle before the main mass of migrants had arrived. Only in West Texas was there any breeding activity after the beginning of October (Fig. 4b). Prior to the arrival of the great masses of migrants, only an occasional monarch has been seen in Texas (Calvert 1993–1997), and communal roosting has not been observed. The early population, which may arrive as early as late August, may differ from the main migrant body in its breeding activity and non-communal roosting. It may not be part of the migratory movement to Mexico. Instead these may be breeding butterflies that have dispersed southward in the same manner that they disperse northward in the spring, stopping to lay eggs as the opportunity presents itself.

The presence of breeding monarchs in Texas in late August and early September was unexpected and requires a rethinking of the pattern of migration. Future studies may show that monarchs regularly breed on Texas milkweeds during September and perhaps October, augmenting their numbers and adding a generation to the monarch life history cycle. The origin of these late summer breeders is of yet undetermined.

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LITERATURE CITED

ANONYMOUS. 1978. Natural regions of Texas, *In* Preserving Texas' Natural Heritage LBJ School of Public Affairs Research Project Report # 31. Compiled by Texas Parks and Wildlife Department, GIS Lab.

———. 1985. Map of the State of Texas. United States Department of the Interior Geological Survey.

———. 1997. Austin rainfall chart. Monthly precipitation records recorded by the National Weather Service at Robert Mueller Municipal Airport. Austin American Statesman, December 7, 1997.

———. 1998. Texas Department of Agriculture, Fire Ant Quarantine Map, TDA Q591D, revised 5-98. Texas Department of Agriculture, Austin, Texas.

ARBINGAST, S. A., L. G. KENNAMER, R. H. RYAN, A. LO, D. L. KARNEY, C. P. ZLATKOVICK, M. E. BONNIE & R. G. STEELE. 1973. Atlas of Texas. Austin: Bureau of Business Research, University of Texas at Austin.

BROWER, L. P. 1985. New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L., pp. 748–785. *In* M. A. Rankin (ed.), Migration: mechanisms and adaptive significance. Contributions in Marine Science. Vol. 27. Marine Science Institute, University of Texas, Port Aransas, Texas.

BROWER, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. J. Lepid. Soc. 49:304–385.

CALVERT, W. H. (1993–1997). Newsletter of the Texas Monarch Watch, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744. vols. 1–3.

CALVERT, W. H. 1996. Fire ant predation on monarch larvae (Nymphalidae: Danainae) in a Central Texas prairie. J. Lepid. Soc. 50:149–151.

CALVERT, W. H. & M. WAGNER. 1999. Patterns in the monarch butterfly migration through Texas and Mexico—1993–1995. *In* Proceedings of the third Monarch Butterflies conference, November, 1997, Morelia, Michoacan, Mexico. In press.

COCKRELL, B. J., S. B. MALCOLM & L. P. BROWER. 1993. Time, temperature and latitudinal constraints on the annual recolonization of Eastern North America by the Monarch butterfly, pp. 233–252. *In* S. B .Malcolm & M. P. Zalucki (eds.), Biology and conservation of the Monarch Butterfly. Publication of the Los Angeles County Museum of Natural History, Los Angeles.

MALCOLM, S. B., B. J. COCKRELL & L. P. BROWER. 1987. Monarch butterfly voltinism: effects of temperature constraints at different latitudes. Oikos 49:77–82.

MALCOLM, S.B., B.J. COCKRELL & L.B. BROWER. 1993. Spring recolonization of Eastern North America by the Monarch butterfly: Successive brood or single sweep migration?, pp. 253–268. *In* S. B. Malcolm & M. P. Zalucki (eds.), Biology and conservation of the Monarch Butterfly. Publication of the Los Angeles County Museum of Natural History, Los Angeles.

MARVIN, C. F. (ED.). 1939. Smithsonian meteorological tables (1931 edition). Lord Baltimore Press, Baltimore.

PORTER, S. D., A. BHATKAR, R. MULDER, S. B. VINSON & D. J. CLAIR. 1991. Distribution and density of polygyne fire ants (Hymenoptera: Formicidae) in Texas. J. Econ. Entomol. 84:866–874.

URQUHART, F. A. 1987. The Monarch Butterfly: international traveler. Chicago: Nelson-Hall.

WOODSON, R. E. JR. 1954. The North American species of *Asclepias*. Ann. Mo. Bot. Gard. 41:1–211.

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